Arctic geese

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Arctic geese: Herbivore-vegetation interaction, predators and human pressures—a symposium synthesis

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A symposium on the Svalbard geese was hosted by the Norwegian Polar Institute in Oslo, Norway, 23–26 September 1997, to collaborate new information on the three goose populations that breed in Svalbard: the barnacle goose *Branta leucopsis*, the light-bellied brent goose *Branta bernicla hrota* and the pink-footed goose *Anser brachyrhynchus*. This paper attempts to synthesise information gained in recent years on these goose populations. Also echoed here are management problems related to these goose populations and priorities for future research.

Looking back over several decades of intensive effort devoted to the goose species breeding in Svalbard, four research themes are touched upon. We argue that (A) unravelling the mechanisms of response of the individual to increasing population density is both technically feasible and theoretically rewarding. A cooperative effort here deserves unflagging priority if we are to achieve population models useful for management purposes. Although individual responses at the various sites utilised through the annual cycle fit the paradigm of density dependence, this does not imply overall population control. The weakest link in the causal chain is (B) understanding the interaction between geese and their food plants, and we contend that this topic should head the new research agenda. This work can profitably be linked with (C) new technologies which allow the tracking of individuals in relation to potential food supplies that can in turn be quantified by means of remote sensing techniques. Under ideal conditions the birds can subsequently be recaptured and profiles of past energetic expenditure reconstructed from indwelling heart-rate loggers. Finally, the geese are not alone, and (D) various predators (notably arctic foxes, polar bears and man) have major impacts on habitat use and influence goose numbers both directly and indirectly, often in an interaction with weather conditions (ice and snow cover). Recently there have been major changes in numbers and distribution of these key predators and at least locally they may now be acting to limit goose populations.

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The density dependence paradigm

For many years the main thrust of avian population studies was to confirm the existence of density dependence (by experiment if possible). Most of the work related to breeding output, clutch size being the best-worked feature. Although by no means universal, the reality of density-dependent checks on breeding is now indisputable (Newton 1998). This allows us to move on to examine the proximate mechanisms that lead to demographic adjustment (for example change in clutch size) and the selective advantage that accrues to the individual that 'obeys the rules' embodied in the density-dependent relationships. From the viewpoint of population management, it is vital to persevere in the study of populations exempt from human hunting pressure until the chain of density-dependent processes at each stage of the annual cycle has been modelled with enough confidence to allow prediction.

Long-term waterfowl studies have similarly revealed the reality of density-dependent effects on reproductive output, and the snow goose studies can serve as our crown witness. Drawing on a massive twenty-year data base on the lesser snow goose *Anser caerulescens caerulescens*, Cooke et al. (1995) noted in their study colony on the Hudson Bay lowland that a long-term decline in clutch size, nesting success, pre-fledgling gosling survival and immature survival have accompanied the overall increase in adult numbers. These changes relate to a decline in food availability in the major salt-marsh feeding areas, reflecting degradation in both the extent and quality of forage available. During the last two decades, survival of the adult breeders has in fact increased, so we are faced with the paradox of conditions conducive to high adult survival and low reproductive output. Habitat degradation in the colony area does not merely reflect a local increase in the nesting goose population, but its extent is directly

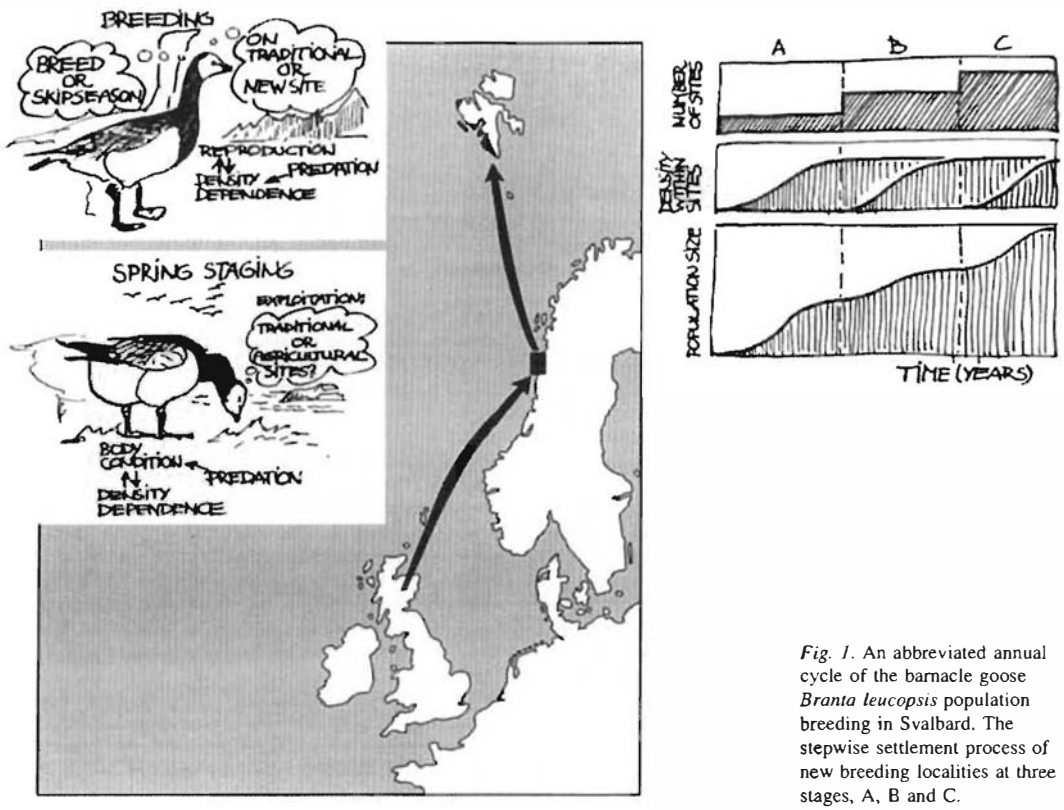

Fig. 1. An abbreviated annual cycle of the barnacle goose *Branta leucopsis* population breeding in Svalbard. The stepwise settlement process of new breeding localities at three stages, A, B and C.

influenced by destructive 'grubbing' activities when geese extract rhizomes from the soil upon arrival in early spring. Many of the birds using the site at that time are in fact passing through on their way further north, and the imbalance between the birds and their breeding habitat reflects the escape of the snow goose population as a whole from the set of checks and balances formerly acting outside the breeding season in the wintering and staging grounds further south. The resulting mismatch is responsible for extensive damage to the salt marsh vegetation of the Low Arctic (Jefferies 1988), not only in the La Pérouse study area but over a widening arc of localities (Jano et al. 1998).

This dramatic demographic upset has engendered a drastic policy shift in North America regarding hunting. Aside from the management problem, the lesser snow goose study underlines the message that in the case of migratory populations, growth of numbers under the vastly increased carrying capacity of the wintering grounds (abundance of suitable agricultural crops) is not necessarily brought under control by density-dependent reductions in reproductive output on the breeding grounds. We must remember that density-dependent mechanisms themselves evolve under the pressure of natural selection on individuals and do not by definition lead quickly to some tidy balance sheet of stable numbers.

The Svalbard barnacle goose

For the barnacle goose *Branta leucopsis*, an abbreviated annual cycle is here depicted and will serve as a frame of reference (Fig. 1). The concentration of the Svalbard barnacle goose in winter and the well-defined spring staging and breeding range provide ideal opportunities for study of population processes (Mehlum 1998, this volume). The gradual, if somewhat piecemeal, accumulation of evidence linking wintering and summering ranges dates from Boyd's (1961) pioneering demonstration that the barnacle goose population with which we are concerned is a separate entity (judiciously deduced from ringing recoveries and the aerial survey of the wintering population 1959/60). Commencing with the spring

staging areas along the Norwegian coast just below the Arctic Circle, we have seen (Prop & Black 1998, this volume) that the choice facing the incoming migrants is to choose between the traditional sites and the more developed, modern agricultural alternatives. This choice is exacerbated by the simultaneous pressures of an increasing goose population coinciding with a deterioration of foraging habitat in the traditional sites due to the progressive abandonment of sheep grazing on the outer islands. Presumably the strong site faithfulness of the experienced individuals reflects the selective advantage of retaining control over choice foraging sites familiar from previous years, but this conservative system can only be maintained if adequate performance is guaranteed in succeeding years. This is one of the features incorporated in the spring staging model (Lang et al. 1998, this volume). Subsequent breeding performance will depend in large part on attainment of adequate body condition. To what extent individual pairs achieve this is liable to reflect a compromise between accepting either the intensive strife at well-visited traditional sites (including frequent disturbance by predators such as sea eagles) or the shift to the new agricultural areas. Prop & Black point to the qualitative differences in the nature of the body reserves accumulated at the alternative feeding sites. The leading question is whether in fact the new alternatives characterised by a lower rate of accumulation of body protein are not in fact a poor second choice, despite the enhanced opportunities for deposition of fat. This point deserves redoubled attention as the data to hand from the spring staging areas offer the tantalising suggestion of a qualitative gate limiting reproductive performance.

Events on the breeding grounds involve a number of choices with a superficial resemblance to events at the staging areas. The choice of the summering (and moulting) site in the first summer visit to the breeding grounds as adolescent prebreeder is liable to impinge on a whole succession of subsequent life history decisions. The future mate is most likely selected from the members of the non-breeding flock which the young bird joins for the summer (Choudhury & Black 1994; Black 1998a, this volume) and prospecting in the local breeding colonies may determine the goal for the next summer. Unfortunately, we do not have access to a rich set of case histories to discern patterns in this phase of intertwined choices, but the evidence to date points to the overriding influence of these early decisions on rates of change in the population as a whole. The first summer appears to be a sort of apprenticeship and represents an exploratory phase which is doubtless under the influence of density-dependence, helping to define for example foraging performance. Recruitment to the breeding colony remains a mysterious process, but we do know that once the individual has bred, the probability is high that it will be faithful to the site.

The overall settlement pattern is visualised as a stepwise process (Fig. 1) where suitable new breeding stations are colonised as a chance process, a few individuals becoming founders of new colonies (Mehlum 1998, this volume). Subsequently the new colony area absorbs increasing numbers (both by accepting immigrants as well as recruitment of young born locally) for some time until levelling off. Taking events along the Nordenskiöldkysten as indicative, local capacity of the summer range for the barnacle goose is limited by the interaction between safe foraging areas (principally lake margins) and predator pressure (nowadays mainly arctic fox *Alopex lagopus*) during the annual moult of the flight feathers (Drent et al. 1998, this volume). The parents (at that time accompanied by their small goslings) are restricted in their habitat use by their extreme vulnerability to predation, and competitive interactions determine which individuals gain access to the limited grazing sites. Foraging grounds are thus a more likely candidate for local population limitation than nesting sites (Tombre et al. 1998, this volume; Mitchell et al. 1998, this volume).

Events at this time cast their shadows ahead because the interplay between predator pressure, forage quality and quantity, and the number of families with which the resource must be shared, set the growth conditions for the goslings (see Loonen et al. in press; Loonen et al. 1998, this volume; Stahl & Loonen 1998, this volume). Not only is early growth vital to ensure survival during the veritable marathon of the fall migratory journey, but since eventual adult body size is also determined at this time, early growth conditions may play an important role in defining performance in later life (through the intermediary of dominance). There must be some competitive filter which the non-breeders (the failed parents and sub-adult hopefuls) must pass through at this time, even though their choice of feeding site

during the flightless period is skewed more towards marginal but safer zones than in the case for families. Provisionally, birds of the various social classes have been lumped together, but obviously more detailed knowledge will be needed to interpret pressures leading to return or emigration and to ascertain if indeed events during the moult play a crucial role in influencing the decision of the next year.

With the increasing number of barnacle geese, declines in both gosling production (Drent et al. 1998, this volume) and adult body size (Black et al. 1998, this volume) have been documented for the intensive study areas, reminiscent of findings in the lesser snow geese. One of the major revelations of our symposium was that these density-dependent effects are locally based (confirming Owen & Black 1989a; Owen & Black 1991) and that they tend to become submerged in a population-wide survey. Taking the data as a whole, the resultant mix of old colony areas (with declining production and growth rate) and new colony areas (temporarily at least released from density-dependent checks) makes it difficult to discern the underlying population processes (Pettifor et al. 1998, this volume). Large inter-annual variation in predator pressure on the breeding grounds further complicates the picture, resulting in highly variable gosling production (Loonen et al. 1998, this volume) not only by direct depredation but also by lowered survival perspectives of the remaining goslings herded together at high density in the relatively predator-safe areas (Stahl & Loonen 1998, this volume). Variable weather conditions in the Arctic (particularly the date of snowmelt, Prop & de Vries 1993) often intervene to mask the underlying density dependence in reproduction. It is comforting to find so many parallels in the reality of density-dependent features in reproduction of the Gotland population of the barnacle goose (Larsson & van der Jeugd 1998, this volume) established in the Baltic as an offshoot of the Russian stock.

Putting migration on the map

Until recently, study of the actual migratory journey linking the areas exploited by the geese at various seasons was a story of inference from before-and-after comparisons attesting to the hazards of the fall migration (Owen & Black 1989b). The implementation of satellite tracking now provides individual migratory trajectories in geese (light-bellied brent geese *Branta bernicla hrota*: Gudmundsson et al. 1995; Clausen & Bustnes 1998, this volume). The findings by Clausen & Bustnes that the light-bellied brent geese breeding in northern Greenland and Svalbard are linked contradict the traditional view that the Greenland birds are linked to the population from Arctic Canada which winter in Ireland. This new information calls for a reassessment of the conservation strategies for the light-bellied brent geese in Europe. In the barnacle goose these devices have been combined with heart rate telemetry culminating in the realisation of the ecologist's dream in providing a record of energetic expenditure en route (Butler & Woakes 1998, this volume). The success of this needle-in-haystack procedure entailing the recapture of the individuals the year after to retrieve the implanted heart rate loggers attests to the unique opportunities provided by the research facility at Ny-Ålesund.

Striving for generality

Lest it be thought that the exigencies of research in the Arctic have prevented us from reaching a satisfactory understanding of the chain of decisions facing the individual up to the time of first nesting, let us turn to the study of the marked shelduck *Tadorna tadorna* population pursued at the Ythan Estuary breeding locality in Scotland by Patterson and his team for upwards of twenty-five years (Patterson 1982; Patterson et al. 1983). The sequence of recruitment to the breeding population in the shelduck consists of progressing through a competitive series of hoops. First, the young bird must compete to enter the non-territorial flock associated with a breeding station. Next, pair formation and territorial behaviour provide access to the breeding population, which at the Ythan study area showed a remarkable stability through two decades of counts. An analysis of population parameters revealed that this stability of the territorial component could only be explained by some density-dependent process limiting entry, most likely in relation to the food resources of the defended site (paired females enjoy exclusive feeding rights during the pre-laying, laying and incubation phase). Patterson speculates that flock size of the non-territorial pool is also limited by competition for resources (such as food or space).

As is the case for geese, density-dependent effects limit hatching and fledging success in the shelduck. Overall, then, the general scheme of events resembles the nested decisions we have adduced for the barnacle goose, but in neither case do we have sufficient data to construct a pathway model quantitatively.

The frustration that disappointed the Patterson team of not being able to balance the local population budget without recourse to immigration (which could not be quantified satisfactorily, particularly with regard to the male sex) is a feature of the barnacle goose study as well. We now realise that detailed observational records at a number of colony areas at the level of detail achieved by Tombre et al. (1998, this volume) for the Kongsfjorden area will be needed to understand relations between them, acting as they do as communicating chambers. The arctic environment has impressed all of us working there with the reality of *extrinsic* controls (notably weather directly and through its impact on the vegetation, and predators) on population processes, and the time has come to dissect the *intrinsic* controls to achieve a quantitative understanding of how competition translates into numbers.

Our new research agenda

Uniting as it did the interests of management and conservation as summarised by Black (1998b, this volume) and Bø et al. (1998, this volume), the agenda served to identify areas where redoubled efforts are needed to satisfy current research demands. In particular, the question was raised if sufficient effort is being devoted to the herbivore-vegetation interaction on the long-term and large scale required to provide early warning of impending change. The rather fragmentary evidence so far from Nordenskiöldkysten points to a redistribution of foraging geese rather than vegetation degradation during the local population rise. There are functional explanations for the lack of a 'trophic cascade effect' engendered by goose grazing on the Spitsbergen range (Loonen & Solheim 1998, this volume). This rather slim line of evidence is congruent with the conclusions on goose-vegetation interactions from the high arctic study of the increasing greater snow goose *A. c. atlantica* population on Bylot Island, Canada (Manseau & Gauthier 1993; Hughes et al. 1994a; Hughes et al. 1994b). These observations reassure us that a major upset on the breeding grounds as witnessed for the lesser snow geese is not imminent (see Abraham et al. 1997) and reaffirms the urgent need for an on-going monitoring effort on the arctic range including vegetation, goose grazing and the interaction with reindeer grazing.

The limited availability of *Zostera*

A suite of papers (Clausen 1998, this volume; Clausen & Percival 1998, this volume; Percival & Anderson 1998, this volume) deal with the behaviour and habitat use of light-bellied brent geese at their wintering sites in Denmark and England. The studies indicate that the *Zostera* beds in the subtidal zone are the preferred feeding areas compared to the adjacent and less productive salt-marshes. It is also suggested that the geese spend less energy as a reaction to disturbance in the *Zostera* beds compared to the other feeding habitats. Water level conditions may restrict the availability of *Zostera* beds, and the geese switch to salt marshes and agricultural land when *Zostera* is scarce.

The diminishing availability of *Zostera* is thought to be the major cause of the shift in winter habitat use by the light-bellied brent geese. The *Zostera* beds have decreased in extent or even disappeared at traditional wintering sites. Also the available *Zostera* beds have been depleted more rapidly during the season due to an increased goose population and by competition with other waterfowl. The cessation of grazing and hay cutting in salt marshes have probably also contributed to make salt marshes less attractive to the geese at some wintering sites. Light-bellied brent geese have recently started using a novel food resource, autumn-sown cereals, as alternative food when the availability of *Zostera* and salt marshes were limited. These changes in habitat use and potential conflicts with agriculture have to be addressed in the management of this goose population.

Population regulation in brent geese

In recent years much information on the Svalbard light-bellied brent population has accumulated. Despite some gaps in the knowledge, we know the locations of its main breeding, wintering and

staging habitats. It is also possible to pinpoint the key resource requirements for survival and fitness-maximisation in these habits. There is still a lack of data on reproductive rates in different parts of its breeding distribution range. However, it is likely that the reproductive rate of the birds breeding at Tusenøyane is a major determinant of the overall population breeding output (Madsen et al. 1998, this volume). Madsen et al. showed that predation, mainly by polar bear *Ursus maritimus*, is a limiting factor in the reproductive success of brent geese at Tusenøyane, and as this factor depends heavily on the seasonal conditions of the sea ice, it is highly erratic. The stochastic character of this predation makes it difficult to construct a predictive population model for management purposes and recalls the uncertainties that have beset modellers of the dark-bellied brent goose *B. b. bernicla* so far.

Behavioural plasticity in pink-footed geese

Most of the recent research on the Svalbard pink-footed goose *Anser brachyrhynchus* population has been conducted by the National Environmental Research Institute in Denmark and collaborators. This research has included a neck-banding programme (started in 1990) and has focused on individual variation in dispersion, migratory strategies and effects on body condition, survival and breeding success. Among the objectives are (1) looking at the effects of hunting on the population (survival impacts), (2) investigating body condition enhancement and migratory strategies at spring staging areas in northern Norway and their effects on fecundity, and (3) examine the influence of stress factors on winter body condition and survival. An important result of this research is that individual variation in migratory strategies, including site-faithfulness at the spring-staging areas in northern Norway, can be documented in terms of fitness-costs. Madsen (1998, this volume) demonstrated nicely the behavioural plasticity of these birds at their spring-staging areas as a trade-off between predation risk and food intake rate. Such behavioural adjustments have allowed the geese to modify migratory routes (and phenology) and even occupy new staging areas, so far without major conflicts with agricultural interests.

Bearing in mind that this is the largest of the three Svalbard goose populations and also the only population subjected to legal hunting, an extension of the research effort seems called for to keep one step ahead of management problems. Recent work has been mainly undertaken outside the breeding season, and consideration should be given to selecting a target area for summer work somewhere in the Svalbard archipelago. We have seen how useful such local studies have been in lending a focus to the work on the other goose species, but admittedly pink-footed geese are by far the most shy and require particularly circumspect methods on the breeding grounds.

Concluding remarks

Conferences tend to close with glowing accounts of future perspectives, and it is a sobering experience to read again Malcolm Ogilvie's masterful summary (Ogilvie 1984) of our previous gathering (1983) and compare the research agenda sketched there with what has actually been achieved. The paramount importance of study of the individual in order to achieve a causal understanding of the processes underlying population dynamics was sounded at that time, stressing the need to trace recruitment of offspring of the focal animals. Unfortunately the accumulation of pedigrees allowing fitness calculations has not kept pace with these vistas, and although we can describe skewness in reproductive performance, we have not yet gained insight as to how this comes about. Again, although the call for more research effort regarding habitat use and habitat selection has been followed through on the spring staging sites in Norway, this has not yet resulted in wider efforts which combine field surveys with the sophisticated remote sensing techniques now available (Jano et al. 1998). The third major thrust from the 1983 meeting was to intensify work on the staging areas and actual travel routes employed during the fall migration, and this work is off to a tantalising start thanks to technological innovation.

We all certainly endorse the view that long-term studies of geese are essential both for applied and theoretical reasons, as argued by Owen & Black (1991), and operationalised by Lang et al. (1998, this volume) as well as by Rowcliffe et al. (1998, this volume). These long-term studies provide the

only road to knowledge of changes in numbers likely in the future. We echo their challenge that 'The changes now taking place in goose populations provide exceptional opportunities to study the way that changes in density affect the individual and the population and the processes by which a population relates to its food resources.'

Acknowledgements. – The cooperative spirit engendered by the joint efforts of an international team under the umbrella of Norsk Polarinstitutt holds promise for the future. We dedicate this contribution to Hugh Boyd, our guide and mentor, in the hope that even in the absence of his editorial touch he will recognise some of the themes he has been developing through the years with his special olympian flavour.

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